

Bee-hawking by the wasp, *Vespa velutina*, on the honeybees *Apis cerana* and *A. mellifera*

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Abstract The vespine wasps, *Vespa velutina*, specialise in hawking honeybee foragers returning to their nests. We studied their behaviour in China using native *Apis cerana* and introduced *A. mellifera* colonies. When the wasps are hawking, *A. cerana* recruits threefold more guard bees to stave off predation than *A. mellifera*. The former also utilises wing shimmering as a visual pattern disruption mechanism, which is not shown by *A. mellifera*. *A. cerana* foragers halve the time of normal flight needed to dart into the nest entrance, while *A. mellifera* actually slows down in sashaying flight manoeuvres. *V. velutina* preferentially hawks *A. mellifera* foragers when both *A. mellifera* and *A. cerana* occur in the same apiary. The pace of wasp-hawking was highest in mid-summer but the frequency of hawking

wasps was three times higher at *A. mellifera* colonies than at the *A. cerana* colonies. The wasps were taking *A. mellifera* foragers at a frequency eightfold greater than *A. cerana* foragers. The final hawking success rates of the wasps were about three times higher for *A. mellifera* foragers than for *A. cerana*. The relative success of native *A. cerana* over European *A. mellifera* in thwarting predation by the wasp *V. velutina* is interpreted as the result of co-evolution between the Asian wasp and honeybee, respectively.

Keywords *Apis cerana* · *Apis mellifera* · Co-evolution · Honeybee · Predation · *Vespa velutina*

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Introduction

Vespine wasps hawk foraging honeybees at their colonies throughout southern Asia (Matsuura and Yamane 1990). Hawking is especially fierce in autumn when the wasps are most populous (Li 1993), and while many native *Apis cerana* colonies succumb to wasp predation, even greater losses are sustained by the introduced European honeybee, *A. mellifera* (Qun 2001; Ken et al. 2005). As is usual in adversarial relationships, both the hunters and the hunted employ strategies of attack and defence. If the wasps come close enough to the entrance of a honeybee nest, more guard bees are alerted, and there is an increased probability of their being killed by heat-balling bees (Ken et al. 2005). Alternatively, under wasp pressure, the bees may simply withdraw into their nests and await heat-balling circumstances to develop. Nonetheless, the wasps continue to seek and attack their quarry as provisions for their own offspring (Sakagami and Akahira 1960; Qun 2001).

Our observations of such encounters included video-recording of wasp hawking methods, success and turnover as well as evasive flying by the bees. There was a great deal of stealth by both wasps and bees. In an area of several metres around honeybee colonies, the wasps display wheeling and jinking flight, hawk the bees and pick them off one at a time, only to be replaced by another hawking wasp. But honeybees may also alter their flight styles to avoid predation. We recorded hawking by the wasp, *Vespa velutina*, on the native honeybee *A. cerana* and the introduced *A. mellifera* to further document such wasp/honeybee encounters including guard bee behaviour, nature of flight of bees, duration of wasp-hawking and the relative success rates of the wasps on both the native and introduced honeybee species.

Materials and methods

Three colonies each of native *A. cerana* and the introduced *A. mellifera* of equal size (four combs of bees) kept in the same apiary were monitored from 10 July to 11 September 2005 in Wuding county, Yunnan Province, China. The numbers of visiting wasps and their hunting success were recorded for 20 to 40 min for each colony on each test day for five test periods giving a total of 23 test days. A digital video camera (Panasonic NV-GS400GC) was placed 1 m in front of the hive entrances to record returning and departing foragers. The flying speed and style were later analysed when the videos were played at a 1/16 lower speed. Flight speed cannot be reliably measured this way, but the time measured is correlated with speed. Flight styles would interfere with this relation. Bees flying in curved trajectories might take a longer time but could fly as fast. Recruited guard bees were counted on stopped frames before, during and after wasp attacks. Foraging bees were monitored in both the presence and absence of hawking wasps.

The recorded behaviours are defined as follows. A visit is simply the appearance of a wasp near the entrance of a beehive that takes up a hawking position. This is a posture in flight with the wasp facing away from the hive entrance to hunt returning foragers. During fine weather, the wasps may hawk from about 0.900 h until about 17:00 h. A “successful hawking visit” indicates that the wasp caught a honeybee. In unsuccessful visits, the wasps fail to catch a honeybee and leave that hive either to find another one or to return to the same one sometime later. Because we could not keep track of individual wasps coming and going, any appearance of a wasp at a hawking post was regarded as a new visit.

Independent samples *t* tests were used to test for differences of *V. velutina* visit frequency and successful hunt rates between both species of honeybee. Two-way repeated measures analysis of variance (ANOVA) and Scheffé multiple comparison procedures were used to test for interspecific and intraspecific differences in the average number of guard bees recruited and flying speeds of bees when exposed to wasps. Homogeneity of the variances between groups was checked using Levene’s test, and a logarithm transformation to the data was used to stabilise the variances where necessary.

Results

The extent of wasp-hawking is shown in Table 1. The rate of wasp-hawking was highest in mid-summer but the frequency per hour of hawking wasps was three times higher at *A. mellifera* colonies ($\bar{x}=21.45$, $SD=11.03$) than at the *A. cerana* colonies ($\bar{x}=7.34$, $SD=1.76$; independent *t* test with $\log[\text{visits/hour}]$: $t_8=3.5$, $P=0.0083$; Levene: $F_{1, 8}=4.45$, $P=0.0679$; Table 1). The wasps were taking *A. mellifera* foragers at a frequency of $\bar{x}=6.13$, $SD=2.62$ per hour, which is eightfold greater rate than $\bar{x}=0.78$, $SD=0.24$ *A. cerana* foragers per hour (independent *t* test

Table 1 Frequency of hawking and hawking success rates of wasps, *V. velutina*, on *A. mellifera* and *A. cerana* honeybees ($N=3$ colonies each)

Date	Species	Observation time (h)	Visit no.	Success no.	Visits/h	Success/h	Success rate (%)
10–16 July	<i>A. mellifera</i> ($n=3$)	14.23	122	40	8.56	2.79	32.59
28–31 July		12.05	250	67	20.75	5.58	26.90
12–16 August		12.32	358	85	29.07	6.90	23.74
24–27 August		26.52	941	265	35.49	9.99	28.16
09–11 September		15.88	213	86	13.41	5.41	40.38
Mean		16.2	376.8	108.6	21.456	6.134	30.354
10–16 July	<i>A. cerana</i> ($n=3$)	15.08	82	8	5.44	0.54	9.93
28–31 July		17.33	123	12	7.08	0.71	10.03
12–16 August		16.32	163	11	9.99	0.67	6.75
24–27 August		22.90	183	19	7.99	0.83	10.38
09–11 September		33.22	206	39	6.20	1.17	18.93
Mean		20.97	151.4	17.8	7.34	0.78	11.20

with log[wasps/hour]: $t_8=8.2$, $P<0.0001$; Levene: $F_{1, 8}=0.37$, $P=0.5616$; Table 1). The hawking success rates of the wasps were about three times higher for *A. mellifera* foragers ($\bar{x}=30.6$, $SD=6.4$ %) and significantly higher than that of *A. cerana* ($\bar{x}=11.2$, $SD=4.6$ %; independent t test: $t_8=5.4$, $P=0.0006$; Levene: $F_{1, 8}=0.81$, $P=0.3941$; Table 1).

In their hawking methods, the wasps take up a position in front of a beehive as its hunting territory flying and wheeling but facing outwards away from the entrance towards returning foragers. The hawking area seems to be territorial because if an area is occupied by a wasp, another entering the area is quickly expelled. The territory of a hawking wasp is about half square meter. However, as soon as a hawking wasp has caught a bee and flown back to its own nest, it replaced within 3 to 7 s by yet another hawking wasp. The daily rhythm of flight by both species of honeybees as well as hawking wasps are the same: high in the morning and afternoon and lowest at mid-day.

During a bout of wasp-hawking near entrances (<1 m) of the *A. cerana* hives ($n=3$ colonies), the average number of guard bees per minute recruited showed a highly significant eightfold increase from $\bar{x}=3.33$, $SD=1.32$ to $\bar{x}=26.78$, $SD=4.32$ (dependent t test: $t_8=15.7$, $P<0.0001$). Similarly, in *A. mellifera* ($n=3$ colonies) the average number of guard bees at the entrance also significantly increased from $\bar{x}=6.11$, $SD=1.83$ to $\bar{x}=9.44$, $SD=2.07$ (dependent t test: $t_8=7.1$, $P<0.0001$). However, guard bee recruitment was significantly higher in *A. cerana* (repeated measures ANOVA—species: $F_{1, 16}=55.9$, $P<0.0001$; with/without wasps: $F_{1, 16}=292.9$, $P<0.0001$; interaction: $F_{1, 16}=165.3$, $P<0.0001$; Levene—without wasps: $F_{1, 16}=2.1$, $P=0.1641$; with wasps: $F_{1, 16}=0.3$, $P=0.6117$). Recruited guard bees of *A. cerana* formed tongue-like groups below the entrances and collectively executed timed waves of shimmering their wings only when wasps directly approached the entrances.

In the absence of any hawking, the average *A. cerana* forager required $\bar{x}=0.35$, $SD=0.06$ s to cover the 1 m distance from the camera to the hive entrance, but this halved to $\bar{x}=0.18$, $SD=0.03$ s during wasp-hawking (dependent t test: $t_9=9.8$, $P<0.0001$, $n=10$ bees for each case). In the absence of hawking wasps, *A. mellifera* foragers were significantly slower flyers because they required an average of $\bar{x}=2.42$, $SD=0.38$ s to cover the 1 m from the camera to the hive. However, when hawking occurred, they even slowed down to $\bar{x}=4.29$, $SD=0.57$ s (dependent t test: $t_9=9.6$, $P<0.0001$, $n=10$ bees for each case), which almost doubled their exposure time to the wasps. Under hawking conditions, *A. cerana* bees cover the 1 m over 20 times faster than do *A. mellifera* (repeated measures ANOVA with log[time]—species: $F_{1, 18}=2179.0$, $P<0.0001$; with/without wasps: $F_{1, 18}=1.3$, $P=0.2776$; interaction: $F_{1, 18}=252.9$, $P<0.0001$; Levene: without

wasps: $F_{1, 18}=0.28$, $P=0.6022$; with wasps: $F_{1, 18}=0.32$, $P=0.5778$). Not only the time to reach the hive entrance changed but also the flight pattern. While *A. cerana* workers put on speed and fly in straight for the entrance, *A. mellifera* workers engage in evasive but slow sashaying manoeuvres like airplanes stacked in a holding pattern.

Discussion

Our observations on hawking wasps and their honeybee quarry illuminate co-evolution in a predator–prey relationship. Indeed, *V. velutina* is a wasp endemic to southeast Asia as is *A. cerana* (Li 1993) while *A. mellifera* was introduced from Europe, where there is no widespread wasp predation. Avoidance of predation by wasps in the two honeybee species is fundamentally different, suggesting substantial predator–prey co-evolution between *A. cerana* and *V. velutina*. While both species kill predatory wasps by heat-balling, *A. cerana* elevates its ball core temperature higher than does *A. mellifera* and also contains more balling bees (Ono et al. 1987, 1995; Ken et al. 2005). In the presence of hawking wasps, *A. cerana* may also withdraw into its nest, which *A. mellifera* does not do. *A. cerana* guard bees also use wing shimmering as a visual pattern disruption mechanism, similar to *A. nuluensis* (Koeniger et al. 1996), which is absent from the behavioural repertoire of *A. mellifera*. These collectively executed timed waves of shimmering their wings, only when the nests are directly approached, appear to be a visual pattern disruption mechanism against predators. In any event, *V. velutina* preferentially hawk *A. mellifera* foragers when both *A. mellifera* and *A. cerana* occur in the same apiary.

Given wasp-hawking, returning *A. cerana* foragers make a very fast bee-line for the hive entrance to avoid the jinking wasps. *A. mellifera* slows down and sashays in the face of wasps. Clearly, this increases the exposure time to the predator and consequently results in more predation success. The success rate of wasps taking *A. mellifera* foragers as prey at three times the rate of *A. cerana* losses is not so surprising, but it points to the fact that *A. cerana* has acquired abilities to partially thwart the predations of the wasps. In conclusion, our comparative study on the honeybees avoiding wasps' predation behaviour demonstrates that *A. cerana* can efficaciously escape from wasp's predation through changing flying behaviour, but *Apis mellifera* cannot.

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